

Distribution of paralarvae and small juvenile cephalopods in relation to primary production in an upwelling area off southern Brazil

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The distribution of paralarvae and small juvenile cephalopods sampled by a rectangular midwater trawl (opening area 8 m²) over the continental shelf off Cape Santa Marta Grande, southern Brazil (28°09'S–29°56'S) during spring 1989 is discussed. An intrusion of Brazil Current Tropical Water (22°C; 36.5) separates warm, less-saline water (22°C; 35.2) from cooler, more-saline water (15°C; 36.4). Prevailing northeasterly winds led to upwelling of South Atlantic Central Water over the shelf, promoting high Chl *a* concentrations. Three species constituted 99% of the 628 cephalopods collected: *Illex argentinus* (*n* = 540; 4–40 mm mantle length, ML), *Argonauta nodosa* (*n* = 46; 2–19 mm ML), and *Loligo sanpaulensis* (*n* = 42, 2–21 mm ML). Segregation of *I. argentinus* juveniles of similar size suggests school formation as small as 10 mm ML. The presence of mature males along with fertilized female *A. nodosa* indicates mating early in life. There was a consistent and direct link between high plankton production and high densities of juvenile cephalopods through a short and ecologically efficient food chain. The relationship between production, pycnocline intensity, and the density of paralarvae and juveniles revealed suitable conditions for survival and growth during the upwelling season.

Keywords: *Argonauta nodosa*, cephalopods, Chl *a*, *Illex argentinus*, *Loligo sanpaulensis*, paralarvae, upwelling.

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Introduction

Understanding the distributional ecology of cephalopod paralarvae in relation to oceanographic process and related plankton production is important in furthering knowledge of the life cycles of these animals. Nevertheless, little information is available on the distribution and abundance of paralarvae and juvenile cephalopods because of their patchy distribution and ability to avoid plankton nets (Vecchione, 1987). The distribution of small juveniles, particularly post-paralarvae, is even less known than that of the paralarvae, making it difficult to investigate the ontogenetic distribution, population dynamics, and life cycle of many species, all of which are necessary for a comprehensive understanding of the importance of cephalopods in marine ecosystems (Vecchione, 1987; Jackson *et al.*, 2008).

The distribution of cephalopod paralarvae tends to be associated with distinct oceanographic features (Rodhouse *et al.*, 1992; Piatkowski *et al.*, 1993; Röpke *et al.*, 1993; González *et al.*, 2005), so environmental conditions have a major influence on both growth and recruitment success (Waluda *et al.*, 2001; Jackson and Domeier, 2003; Otero *et al.*, 2008). For example, on the northwest Iberian shelf, an increase in abundance and biomass of *Octopus vulgaris* paralarvae was significantly correlated with the simultaneous decrease in water-column-integrated nutrients and Chl *a* concentrations (Otero *et al.*, 2009). Additionally, the

significance of food availability as a major regulator of survival and growth of squid paralarvae has been validated through laboratory studies (Vidal *et al.*, 2006), demonstrating that paralarvae react rapidly to changes in the environment.

The Sardine and Anchovy Recruitment Project (SARP) was aimed at understanding the physical and biological processes that influence recruitment of anchovy (*Engraulis anchoita*) and sardine (*Sardinella brasiliensis*) in the southwest Atlantic Ocean (SAO). To achieve this goal, three areas were chosen in the SAO based on their proximity to the subtropical convergence, different hydrography, and the presence of *E. anchoita* and *S. brasiliensis* larvae (Alheit, 1989). One of the areas chosen was Cape Santa Marta Grande in southern Brazil (29°S), where there is a steep, narrow shelf (90 km), favouring subsurface upwelling of nutrient-rich subtropical water, also known as South Atlantic Central Water (SACW). This water mass can upwell into subsurface waters throughout the year, but is most prevalent during spring and summer, when Brazil Current (BC) Tropical Water (TW) penetrates farther over the shelf, above SACW, leading to the formation of cyclonic eddies and the enrichment of the whole tropic chain (Odebrecht and Djurfeldt, 1996; Campos *et al.*, 1999).

The warm BC originates in the South Equatorial Current, turns along the coast of central Brazil, and contours the curvature of the

coastline between Cabo Frio (23°S) and Cape Santa Marta Grande (Lima *et al.*, 1996; Campos *et al.*, 1999). The BC is important in the life cycle of the squid *Illex argentinus*, which is found in the SAO (20–55°S) and has been one of the most fished cephalopods in the world for the past three decades (Csirke, 1987; Haimovici *et al.*, 1998). High densities of newly hatched paralarvae of this species were recorded in spring off Cape Santa Marta Grande (Vidal, 1994a) and in nearly all seasons in the extreme south of Brazil (Haimovici *et al.*, 1995), indicating the location of its spawning grounds and nursery areas. Here, patterns of distribution and density of paralarvae and small juvenile cephalopods collected during the SARP are examined in relation to oceanographic processes and primary production off Cape Santa Marta Grande during spring 1989.

Material and methods

Cephalopod paralarvae and small juveniles were collected by the German research vessel RV "Meteor" during SARP cruise 11, leg 3. The survey took place between 19 and 26 November 1989 off Cape Santa Marta Grande area (28°09.5'–29°56.5'S).

Three transects were conducted perpendicular to the coast (northern, central, and southern), with five stations each (Figure 1). Typically, three oblique hauls were conducted at each station, ~15 per transect, totalling 40 hauls, distributed between the 30 and 146 m isobaths. The stations were 5 nautical miles (hereafter miles) apart, and the distance between each transect was 30 miles (Figure 1). A rectangular midwater trawl with an opening area of 8 m² (RMT8) and 1-mm mesh size in the codend was deployed. The net proved to be an efficient sampler of small juveniles of many fish species (Kinzer and Schulz, 1985). The samples were collected in oblique hauls from near the bottom to the surface at a constant speed of 2.5 knots. Therefore, cephalopods may have been caught anywhere in the water column sampled. Between the hauls, *in situ* phytoplankton fluorescence was measured and CTD casts carried out every 5 miles over the whole grid of stations (Nellen, 1990). Cephalopods in the samples were immediately fixed in buffered

7% formaldehyde–seawater and preserved in buffered 4% formaldehyde for subsequent identification, following Nesis (1987). Dorsal ML of the smallest specimens was measured to the nearest 0.05 mm in a stereoscopic microscope equipped with an ocular micrometer, and the largest juveniles were measured with a paquimeter to the nearest 0.1 mm. The relative abundance at all positive stations was standardized to the number of individuals per 100 m³ of water volume filtered. The volume filtered was estimated indirectly by multiplying the area of the mouth of the net by the towed distance.

Oceanographic conditions

Summary information on the oceanographic conditions and primary production (Nellen, 1990) and on phytoplankton size structure (Odebrecht and Djurfeldt, 1996) during the cruise is used here to describe the main oceanographic features of the survey. The vertical profiles of water temperature, salinity, and density were similar for the three transects and are therefore only shown for the southern transect (Figure 2). An intrusion of BC TW was recorded between 20 and 40 m, separating warm (21–22°C), less-saline water (34.7–35.2) at the surface from cooler (15–17°C), more-saline water (36.6) at the bottom, resulting in pronounced thermal stratification (Figures 2a and b). This caused a double pycnocline in the water column, the first over the TW intrusion and the second one under it. The inclination of the isopycnals indicated SACW upwelling on the shelf, caused by prevailing northeasterly winds (Nellen, 1990; Figure 2c).

At the coastal stations of the northern transect, temperature decreased gradually from 21°C to 18°C at 15 m, and Chl *a* concentrations were modest (1.0–2.0 mg m⁻³) throughout the water column. At the midshelf stations, however, a strong subsurface Chl *a* maximum layer (SCM) was registered below the intrusion of TW at the base of the thermocline, which lay between 25 and 45 m deep. At the SCM, Chl *a* concentrations reached 6.00 mg m⁻³ (Nellen, 1990). At the outer stations, there was a steep thermocline at about 50–80 m deep, with the temperature decreasing steadily from 22°C to 16°C (Figure 2a); peaks of Chl *a* (5.8 mg m⁻³) were also recorded 50–60 m deep (Nellen, 1990).

Most of the coastal stations of the central transect revealed steep thermoclines and haloclines about 10–35 m deep (Figure 2), and intermediate levels of Chl *a* (2.90 mg m⁻³) were recorded between 32 and 40 m. At most midshelf and outer stations, a double (10–40 m) or even a triple thermocline was observed (10–100 m), with the lowest (0.5–2.5 mg m⁻³) and deepest (62–90 m) concentrations of Chl *a* and both temperature and salinity indicating the presence of SACW.

At coastal stations of the southern transect, temperature (21°C) and salinity (35.30) were uniform and the water column was homogenous in terms of vertical structure, with low concentrations of Chl *a* (0.50–1.50 mg m⁻³). At midshelf stations, low levels of Chl *a* were recorded throughout the water column (1.00 mg m⁻³), except a peak at 2.00 mg m⁻³ between 38 and 45 m, coinciding with the thermocline. At the outer stations, temperature decreased from 22°C to 18°C and there was a thermocline between 50 and 80 m (Figure 2a), where Chl *a* concentrations of 1.60 mg m⁻³ were registered.

Results

In all, 628 cephalopods were collected. Four taxa could be identified to species, one to genus (*Aburropsis* sp.) and one to family (Psychroteuthidae; Table 1). *Illex argentinus* was the most

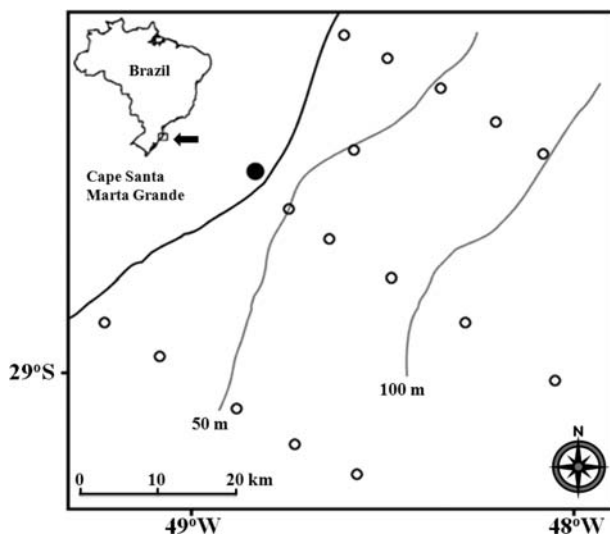


Figure 1. Area sampled by the RV "Meteor" between 19 and 26 November 1989 off Cape Santa Marta Grande, southern Brazil. Open circles are the sampling stations.

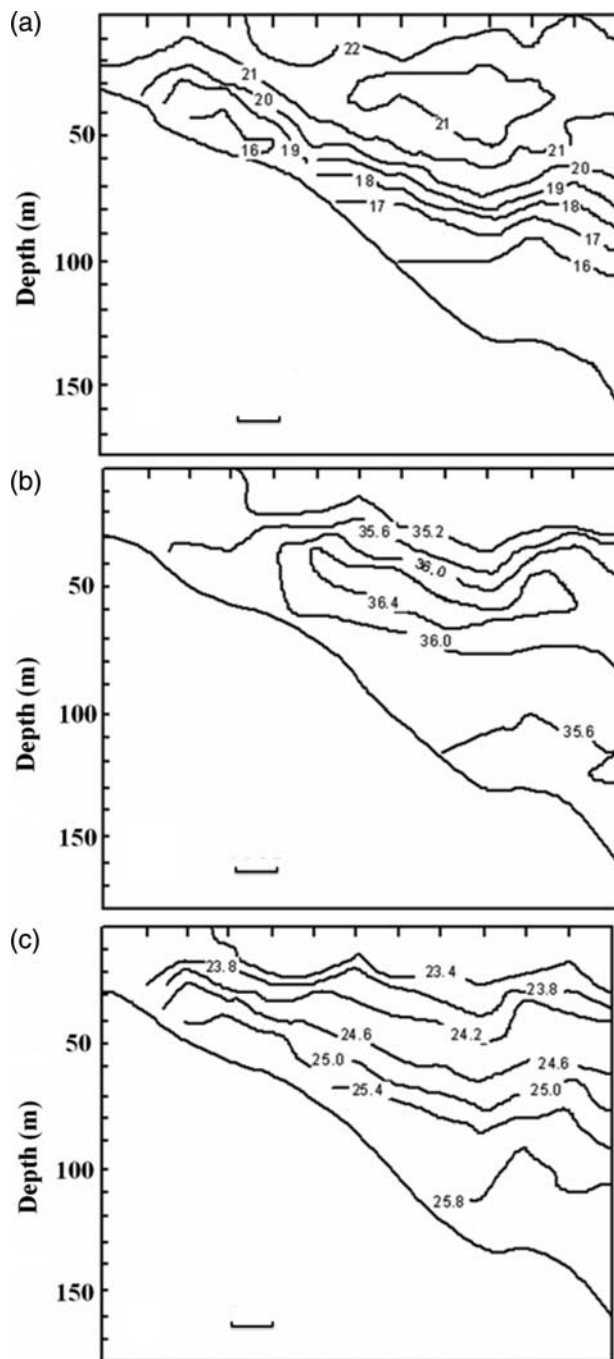


Figure 2. (a) Temperature ($^{\circ}\text{C}$), (b) salinity, and (c) σT distribution along the southern transect off Cape Santa Marta Grande. The scale represents 5 nautical miles.

abundant cephalopod caught, accounting for 86% of the total cephalopod catch. *Argonauta nodosa* was the next most abundant (7.2%), followed by *Loligo sanpaulensis* (6.7%). Just one or two specimens of all other cephalopod taxa were captured (Table 1).

Illex argentinus

Illex argentinus paralarvae and juveniles were distributed over almost the entire sampled area between the 46 and 112 m isobaths (Figure 3a). In all, 540 were collected in 17 of the 40 hauls carried

out, and the ML ranged from 4.0 to 40 mm with a mean of 15.3 mm (Table 1). Of all those collected, 6.4% were rhynchoteuthion paralarvae of 4.0–7.8 mm ML (mean 5.94 mm) and 93.4% were juveniles of 8.0–26.0 mm ML (mean 15.9 mm), except for one of 40 mm ML (Table 1). Larger juveniles (>16 mm ML) were mainly present midshelf over the northern and central transects, whereas rhynchoteuthion paralarvae were caught both close to the coast and farther offshore and dominated the southern transect. The species was absent from coastal stations in the southern transect, where the water column was homogeneous and low Chl *a* concentrations were registered, and from offshore stations of the northern and central transects with their greater mixed-layer width (Figures 2 and 3).

Densities peaked in the northern transect, and the highest density of 8.54 squid per 100 m^3 was registered midshelf 70 m deep (Table 1, Figure 3), where 413 juveniles (67% of the total; mean 16.3 mm ML) were caught at sizes ranging from 10 to 18 mm ML. At that station, there was a steep thermocline between 20 and 45 m, where the temperature decreased from 20°C to 16°C . The maximum density of juveniles there coincided with the highest concentrations of Chl *a* (6.0 mg m^{-3}) recorded during the whole survey, located below the intrusion of TW, in the lower part of the thermocline (35–45 m).

At stations of the central transect, densities ranged from 0.022 to 0.073 squid per 100 m^3 , mainly rhynchoteuthion paralarvae and small juveniles <15 mm ML (Figure 3a). The water column was stratified, with a sharp drop in temperature from 22°C to 16°C and a double thermocline at 8–10 and 30–44 m. Chl *a* concentrations varied from 1.0 to 2.30 mg m^{-3} between 35 and 50 m deep. On the southern transect, the maximum density was 0.075 squid per 100 m^3 , mainly rhynchoteuthion paralarvae. The temperature at the stations where the paralarvae were caught ranged between 19°C and 21°C , and Chl *a* concentrations were among the lowest (0.40 mg m^{-3}) in the whole survey, except a peak of 2.00 mg m^{-3} between 32 and 35 m deep.

Loligo sanpaulensis

In all, 42 *L. sanpaulensis* were caught in 11 of the 40 hauls, distributed between the 46 and 77 m isobaths (Figure 3b). None were found at the offshore stations or in the southern transect at bottom depths <43 m. The size range taken was 2.0–21.5 mm ML (mean 9.1 mm ML; Table 1), and the mode was 6.0–8.0 mm ML. There was no spatial pattern in the density and no consistent pattern of size distribution.

On the northern transect densities were between 0.0093 and 0.0518 squid per 100 m^3 and were associated with steep, shallower thermoclines between 20 and 40 m deep and average Chl *a* concentrations. Most were caught in the central transect (0.166 squid per 100 m^3 ; Figure 3b), at stations associated with a sharp drop in temperature (22 – 16°C) and double pycnoclines. At those stations, small paralarvae and juveniles were found together, and Chl *a* concentrations varied between 1.0 and 2.30 mg m^{-3} between 35 and 50 m deep. On the southern transect, *L. sanpaulensis* was taken at just one station, a catch rate of 0.0375 per 100 m^3 , where the oceanographic conditions were the same as described above for *I. argentinus*.

Argonauta nodosa

A total of 46 specimens of *A. nodosa* was caught in 14 of the 40 hauls, distributed over almost all the sampled area between the 43 and 125 m isobaths (Figure 3c).

Table 1. List of species, numbers, size ranges, and densities of paralarvae and juvenile cephalopods collected by a rectangular midwater trawl (RMT8) off Cape Santa Marta Grande, southern Brazil.

Taxon	Species	n	ML size range (mm)	Mean mantle length (ML, mm)	Number of individuals per 100 m ³
Myopsida					
Ctenopterygidae	<i>Ctenopteryx sicula</i>	1	3.0	–	0.0084
Loliginidae	<i>Loligo sanpaulensis</i>	42	2.0–21.5	9.1	0.0084–0.1680
Oegopsida					
Enoploteuthidae	<i>Abraliopsis</i> sp.	2	4.0	–	0.0081–0.0113
Ommastrephidae	<i>Illex argentinus</i>	540	4.0–40.0	15.3	0.0081–8.5330
	Rhynchoteuthion paralarvae	35	4.0–7.8	5.9	0.0084–0.0787
	Juveniles	505	8.0–40.0	15.9	0.0100–5.6200
Psychroteuthidae	Not known	1	–	–	0.0081
Octopoda					
Argonautidae	<i>Argonauta nodosa</i>	46	2.0–19.0	8.2	0.009–0.2100
	Males	21	2.0–6.8	5.3	0.010–0.0410
	Females	25	4.2–19.0	10.6	0.009–0.0560

ML ranged from 2.0 to 19.0 mm (mean 8.2 mm), and length frequencies showed that the mode was at 4.0–6.0 mm. Females of 4.2–19.0 mm ML (mean 10.6 mm) represented 60.9% of all those caught, and male ML was 2.0–6.8 mm (mean 5.3 mm; Table 1). The largest females had well-developed dorsal arms but no shell, but examination of their mantle cavity revealed the presence of hectocotyli in 54% of females >16 mm ML. Some 41% of the males had well-developed hectocotyli, indicating advanced or complete sexual maturity. Males and females were found together at most of the stations, with no apparent pattern in size or sex distribution, although the smallest specimens (<3 mm ML) were generally taken at bottom depths >99 m. There was a consistent trend of higher density midshelf over all three transects. Density peaked at 0.21 argonauts per 100 m³ over the shelf of the northern transect at bottom depths between 55 and 77 m, where females of 12–19 mm ML dominated (Figure 3c). On the northern transect, *A. nodosa* was caught mainly at the same stations as *I. argentinus*, and on the central transect, it also coincided with the presence of *L. sanpaulensis*. The oceanographic conditions of the stations at which this species was caught were characterized by sharp pycnoclines and high concentrations of Chl *a*. On the southern transect, however, the species was more abundant than the other species, and males dominated. At those stations, the thermocline was between 20 and 35 m, with temperature decreasing from 21°C to 19°C, and Chl *a* concentrations ~2.00 mg m⁻³ between 33 and 38 m deep.

Other species

One *Ctenopteryx sicula* of 3.0 mm ML was collected on the southern transect at a station 62 m deep (Table 1). There, a sharp thermocline was found between 25 and 45 m deep, with temperature decreasing from 21.5°C to 18°C, and a Chl *a* concentration of 2.00 mg m⁻³ was recorded 35–45 m deep. Two *Abraliopsis* sp. (4.0 mm ML) were caught at the deepest station in the northern (99 m) and southern transects (80 m). One psychroteuthid was caught at the same station as *Abraliopsis* in the northern transect, but unfortunately was damaged and additional taxonomic details could not be obtained.

Discussion

There is growing evidence that paralarvae and juvenile cephalopods of many species are associated with seasonal events of plankton production, although few studies have demonstrated a direct

effect of upwelling blooms on the distribution and abundance of paralarvae (Rocha *et al.*, 1999; Sauer *et al.*, 2002; González *et al.*, 2005; Otero *et al.*, 2009). During this study off southern Brazil, a consistent and direct relationship between elevated phytoplankton production and high densities of *I. argentinus*, *L. sanpaulensis*, and *A. nodosa* small juveniles was established in a subsurface upwelling region off Cape Santa Marta Grande. The largest catches of juveniles of these species were made over the midshelf, at stations characterized by sharp pycnoclines resulting from the contact of TW at the surface with cold, nutrient-rich SACW at the bottom, which led to the formation of a strong SCM at the base of the thermocline. No cephalopod catches were made at the two coastal stations in the southern transect, where the water column was homogeneous and concentrations of Chl *a* were low. These results confirm the findings of Röpke *et al.* (1993) that pycnoclines can be associated with peaks in primary production and concentrations of cephalopod paralarvae and fish larvae in the Arabian Sea.

Off Cape Santa Marta Grande, nearshore mixing caused by turbulence-driven bottom friction, during both upwelling and downwelling of SACW, influenced phytoplankton production and size structure during the survey (Odebrecht and Djurfeldt, 1996). Those authors observed that 85% of the subsurface Chl *a* maximum layer was microphytoplankton (cells >20 µm, mainly *Coscinodiscus* sp. and *Thalassiosira* sp.), whereas at the surface and also at oceanic stations, most of the Chl *a* was contributed by nanoplankton (1–20 µm) and picoplankton (<1 µm). Hence, fertilization of the euphotic zone with the SACW leads to subsurface growth of large diatoms, providing optimal food for secondary consumers. Paralarvae and juvenile cephalopods feed directly on secondary production as second-level consumers (Passarella and Hopkins, 1991; Laptikhovskiy, 2002). The coupling between sufficiently long peaks of primary production through this short and ecologically efficient food chain would allow juvenile cephalopods to grow and to form dense patches. Indeed, an exceptionally high density of *I. argentinus* juveniles was caught in the middle of the northern transect at exactly the same station at which the highest concentration of Chl *a* was registered (6.0 mg m⁻³). Notably, there was little variation in size between these juveniles, given that the ML of 67% of the total caught ranged between 10 and 18 mm. This result provides compelling evidence that *I. argentinus* as small as 10 mm ML already swim in schools to forage. The occurrence of a school of small juvenile

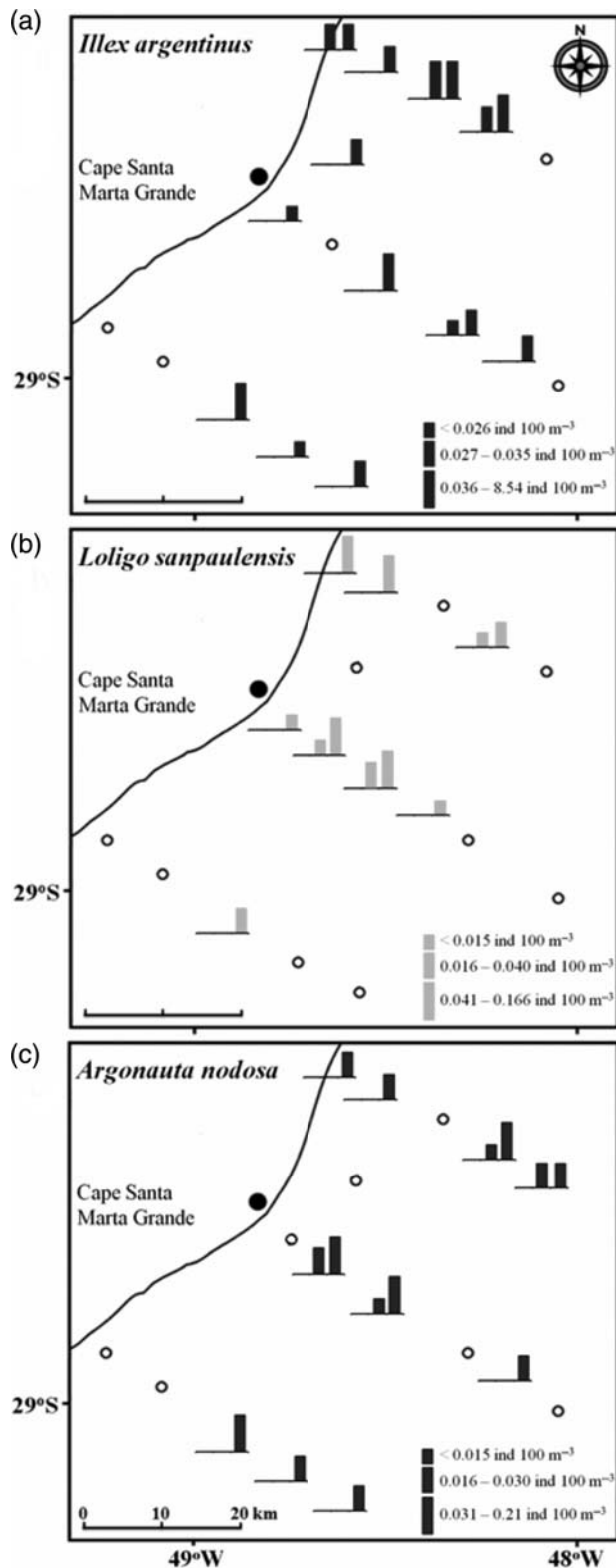


Figure 3. Distribution and density of paralarvae and small juvenile cephalopods off Cape Santa Marta Grande: (a) *I. argentinus*, (b) *L. sanpaulensis*, and (c) *A. nodosa*. Three hauls were carried out at each station and each bar represents the density per haul (number of individuals collected per 100 m³ of filtered water). Open circles signify that no catch was made at that particular station.

I. argentinus directly linked to elevated plankton production is a novel finding and supports the notion of O'Dor (1998) that rapid growth of ommastrephid juveniles would allow individuals of a school to track a peak of production through time, exposing them to similar environmental and feeding conditions.

The ability to swim in schools requires specific morphological features and may confer advantage to individuals in the school, by improving the chances of finding and exploring patches of plankton production, enhancing growth, and survival. Vidal (1994b) found a major discontinuity in the allometric growth of arms, head, and eyes in juvenile *I. argentinus* of 14–17 mm ML, coinciding with the formation of eight rows of suckers on the dactylus and an increase in the number of chromatophores in the body. Sharp morphological changes may signal critical limits in the development related to key behavioural events. Therefore, it is likely that the morphological changes observed in post-paralarvae of *I. argentinus* were related to the formation of schools, because schooling squid need to be equipped with improved vision (eyes) and communication (chromatophores) skills, as well as functional clubs. Additionally, the formation of schools seems to depend on size rather than age, because the ability of individual squid to swim against a current is crucial (Hurley, 1978). In *Doryteuthis opalescens* reared at 16°C, the formation of schools was first observed in squid 35–45 days old and 6–8 mm ML. The schools were formed by squid of similar size and situated where the current was at its maximum (EAGV, pers. obs.). It seems that there is a similarity between the sizes and ages at which both *D. opalescens* and *I. argentinus* swim in schools. Arkhipkin (1990) estimated that *I. argentinus* juveniles of 15–19 mm ML would be around 50–60 days old, so 10 mm ML juveniles would be even younger.

Loliginid squids are commercially exploited along the southern coast of Brazil (23–34°S). A study of the distribution and abundance of *L. sanpaulensis* between 30°40' and 34°30'S showed spawners to be present year-round (Andrigetto and Haimovici, 1991), and small loliginid paralarvae (<1.7 mm ML) were found <20 m deep around Santa Catarina Island (27°47'18"S 48°31'07"W; Martins and Perez, 2006). During the survey reported on here, *L. sanpaulensis* paralarvae and juveniles were most abundant in coastal and midshelf waters <55 m deep, at stations with double pycnoclines and low-to-moderate concentrations of Chl *a*. It is of note that juveniles of *L. sanpaulensis* and *I. argentinus* differed in peak density between stations, and consequently in habitat utilization. The two species may be responding differently to certain oceanographic features, such as temperature and salinity.

The life cycle and distribution of *A. nodosa* in the southwestern Atlantic is poorly understood. However, there is evidence indicating that they are fairly abundant. Off southern Brazil, argonautid beaks are common in the stomach contents of demersal and pelagic fish, marine mammals and birds (Vaske and Castello, 1998; Vaske and Rincón-Filho, 1998; Santos and Haimovici, 2002). Nevertheless, the results of this study have provided important information on the distribution and life cycle of this species. Juveniles, mainly females, were caught midshelf under the influence of SACW and high concentrations of Chl *a*, and early paralarvae (< 3 mm ML) over the outer shelf under the influence of BC TW. Mature males (4.0–6.8 mm ML) with fully developed hectocotyli were caught at the same stations as juvenile females (11–19 mm ML). Moreover, hectocotyli were found inside the

mantle cavity of 54% of females of 16–19 mm ML, indicating mating early in life. This information provides detail of the reproductive strategy of argonauts and goes some way towards answering intriguing questions on how nektonic females and planktonic males would overcome the challenges of finding mates in the pelagic realm and mate, considering the different body dimensions of the two sexes. Observations on chains of shelled female *A. hians* and *A. boettgeri* in the Indian and western Pacific Oceans (Nesis, 1977) and of *A. nouryi* in the eastern tropical Pacific lead to the suggestion that such behaviour could enhance the conspicuousness of females as a strategy to increase the rates of mate encounter in the open ocean (Rosa and Seibel, 2010). The results of the present study have demonstrated for *A. nodosa* that copulation takes place when males and females are of similar size and gather in nursery areas. In this environment, the chances of encounter between males and females increase, and the effectiveness of mating efforts is likely improved by the similar size of the two sexes. The presence of hectocotyli in the mantle cavity of *A. boettgeri* small females was also observed by Nesis (1977). Considering that females as small as 16 mm ML have mated, this suggests that they must mate several times during their life, whereas males likely have a very short life cycle. These findings raise questions about the reproductive strategy of argonauts related to the storage of hectocotyli and the maturation size of females.

Few conclusions can be drawn from the other species caught. However, it seems likely that *Ctenopteryx sicula* and *Abraliopsis* sp., along with the psychroteuthid, could have penetrated farther over the shelf under the influence of SACW.

The RMT8 net used proved to be suitable for collecting large paralarvae and small juvenile cephalopods in the size range 6–20 mm ML. One of the advantages of the net is that its mouth area (8 m²) is considerably larger than that of traditional plankton nets. The towing bridles and release gear are not directly in front of the mouth, and the net is made of black mesh. Considering that cephalopods are very effective at avoiding nets (Vecchione, 1987), these features may reduce net visibility and avoidance. The RMT8 also effectively sampled large numbers of small juvenile cephalopods over the Falklands shelf in the southwestern Atlantic (Rodhouse *et al.*, 1992) and during the survey off Cape Santa Marta Grande proved effective at sampling *E. anchoita* larvae >15 mm standard length (Castello and Vasconcellos, 1995). However, there may be some bias, because the nominal mouth area of the RMT8 depends on the mouth angle during towing, and the nominal area is only attained when the mouth angle is 45° (Roe *et al.*, 1980). According to those authors, the mouth angle remains constant between speeds of ~2.6–8.0 knots, so was in accord with the towing speeds deployed during the present survey.

Given the limited knowledge of the ecology of paralarvae and small juvenile cephalopods, the results presented here have provided new information with which to assess the distribution pattern of important stages of the life cycles of *I. argentinus*, *A. nodosa*, and *L. sanpaulensis*. The presence of a wide range of sizes of paralarvae and small juveniles of these species off Cape Santa Marta Grande is almost certainly attributable to the existence of suitable nursery grounds that combine high primary and secondary productivity in short and efficient food chains with appropriate retention mechanisms and survival conditions. Although the results obtained were derived from a particular small region, they have value in expanding the currently limited

knowledge of the direct effects of upwelling on the distribution and abundance of cephalopod early life stages. Upwelling phenomena may, in fact, be one of the main regulators of the availability of food to early life stages of cephalopods and of their growth, survival and recruitment.

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